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Lisa A. Solinger

*Washington University in St. Louis*

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WASHINGTON UNIVERSITY IN ST. LOUIS

Department of Psychological & Brain Sciences

The Effect of Incentives on Pupil Dilation During Recognition Memory:  
An Attentional Saliency Account of the Pupil Old/New Effect

by

Lisa A. Solinger

A thesis presented to  
The Graduate School  
of Washington University in  
partial fulfillment of the  
requirements for the degree  
of Master of Arts

May 2017  
St. Louis, Missouri

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*May 2017*



## ABSTRACT OF THESIS

The Effect of Incentives on Pupil Dilation During Recognition Memory:

An Attentional Saliency Account of the Pupil Old/New Effect

by

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Master of Arts in Psychological & Brain Sciences

Washington University in St. Louis, 2017

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A robust finding in eye tracking studies of recognition memory is that correctly recognized studied (i.e., old) items yield greater pupillary dilation (PD) than do correctly identified unstudied (i.e., new) items. Termed the pupil old/new effect, it is generally thought to reflect the cognitive effort involved in retrieving content from memory. However, there is evidence suggesting that the PD response reflects the attentional salience of retrieval, and not retrieval processes per se (Mill, O'Connor, & Dobbins, 2016). To adjudicate between these two accounts, I crossed performance-based incentives with “new” and “old” conclusions—systematically controlling whether the detection of new or old items was more motivationally salient. During baseline, subjects demonstrated the classic pupil old/new effect. However, when “new” conclusions were incentivized the effect was eliminated, and when “old” conclusions were incentivized the effect was amplified relative to baseline. Thus, the early amplitude PD response does not track memory strength or retrieval per se. Instead, it captures a recognition orienting component that can be modulated via incentives. In addition to this early pupillary component, a subjective uncertainty component differentiated low- versus high-confident responses, and a goal-contingent component showed a late dilation response when subjects rendered incentivized responses. The findings support the attentional salience account of the pupil old/new effect and

reveal additional distinct psychological contributors to the PD response during recognition memory.

# **Chapter 1: Introduction**

A robust finding in eye tracking studies of recognition memory is that correctly recognized studied items yield greater pupillary dilation (PD) than do correctly identified unstudied items, a phenomenon termed the pupil old/new effect (Võ et al., 2008; see also Goldinger & Papesh, 2012; Gomes, Montaldi, & Mayes, 2015; Kafkas & Montaldi, 2015; Otero, Weekes, & Hutton, 2011). Given that the fundamental difference between recognizing old and new items is the presence of episodic content for old material, it is generally thought to signal the successful retrieval of episodic content (Goldinger & Papesh, 2012). Specifically—and consistent with other prominent work linking PD to cognition (Beatty & Kahneman, 1966; Kahneman, 1973)—researchers suggest that this effect reflects the increased cognitive “load” or effort incurred when episodic content is successfully retrieved (Granholm, Asarnow, Sarkin, & Dykes, 1996; Kahneman & Beatty, 1966).

In addition to finding a robust old/new effect, researchers have shown that this effect consistently increases as a function of the strength of the memory signal. Specifically, larger pupil dilation has been reported for remember versus know judgments (Otero, Weekes, & Hutton, 2011), high versus low confidence ratings (Naber, Frässle, Rutishauser, & Einhäuser, 2013), deep versus shallow encoding (Brocher & Graf, 2016; Otero et al., 2011), and high versus low frequency words (Montefinese, Ambrosini, Fairfield, & Mammarella, 2013). Taken together, these studies converge on the idea that PD during recognition memory actually indexes the strength of the underlying memory signal. In fact some researchers claim that PD provides a “veridical” measure of prior experience (Goldinger & Papesh, 2012; Hannula, Baym, Warren, & Cohen, 2012; Heaver & Hutton, 2011). Based on this logic, researchers use pupillometry to

examine memory in populations that are typically challenging to study, including preverbal infants (Jackson & Sirois, 2009) and amnesiacs (Laeng et al., 2007).

However, these memory specific accounts of the pupil old/new effect, tacitly assume that the motivational significance of making “old” and “new” decisions is similar. While that may be the case, it is also possible that subjects are internally motivated to maximize the detection of studied materials (see Han, Huettel, Raposo, Adcock, & Dobbins, 2010). Specifically, subjects might value “old” more than “new” responses based on a reasonable belief that the primary goal in a recognition memory task is to maximize the detection of studied items. If subjects value “old” more than “new” conclusions, then the pupil old/new effect might, in fact, reflect the attentional saliency of old relative to new items. Indeed, the idea that attentional saliency regulates the pupil old/new effect was recently introduced by Mill, O'Conner and Dobbins (2016). They used an explicit cueing paradigm to demonstrate that the pupil old/new effect was modulated by participants' expectations and not memory retrieval per se. Whereas Mill et al. used explicit cueing to manipulate attentional saliency, in the current study, I sought to extend their findings by manipulating attentional saliency with performance-based incentives.

To test the idea that the pupil old/new effect reflects participants' intrinsic motivation to detect old more so than new material (and not simply the oldness of the materials), I used an extrinsic reward manipulation to systematically control the motivational salience “old” and “new” conclusions, effectively shifting the participants' goal from maximizing the detection of old items to maximizing the detection of new items (Han et al., 2010; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002). If the attentional saliency account holds true, then PD during recognition will depend upon which response type is emphasized as important. In contrast, if the

memory specific account is correct, then PD will be greater for old compared to new items regardless of the extrinsic contingencies placed upon response types.

In the remainder of the introduction I review the two studies that have directly motivated the current work: Mill, O’Conner and Dobbins (2016) introduced above; and secondly, a study conducted by Han et al. (2010) that investigated the functional significance of striatal activations during recognition decisions using a paradigm that motivated the design of the current study. I conclude by explaining how manipulating incentive during recognition pits memory specific and attentional saliency accounts of the pupil old/new effect against one another.

## **1.1 The Pupil Old/New Effect: Evidence of an Attentional Saliency Account**

In a recent study, Mill, O’Conner and Dobbins (2016) tested the idea that PD during recognition does not reflect the retrieval of memorial content per se, but the attentional significance of recognition retrieval. As a test of this general idea, they manipulated observers’ expectations during typical verbal recognition memory testing by pre-cueing each recognition memory probe using either “Likely Old”, “Likely New”, or uninformative ‘????’ cues. The cues were 70% valid. They demonstrated that the cues moderated the pupil old/new effect as a function of altering the subjects’ expectations. In the case of uninformative cues the typical pupil old/new effect was observed. However, when observers were given the “Likely Old” cue the effect was completely eliminated, meaning that when recognition was expected, there was no evidence of a pupil old/new effect. In contrast, when observers were given the “Likely New” cue, and hence did not expect recognition to occur, there was a robust pupil old/new effect that was considerably larger than during uncued trials. Thus the presence or absence of the pupil old/new effect was shown to be completely mediate by actively manipulating subjects’

expectations regarding the likelihood of recognition. The findings suggest that the pupil old/new effect depends, not on an item's prior occurrence, but on the attentional significance or salience of recognition given the context. Moreover, the same pattern was obtained regardless of whether observers' old or new conclusions were correct or incorrect and thus it reflects their subjective perception of recognition, not veridical recognition.

## **1.2 Motivational Significance of Rendering Old/New Responses**

In the current project, we further test the attentional saliency explanation of the early pupil old/new effect. Whereas Mill, O'Connor and Dobbins (2016) used explicit cues to manipulate subjects' expectations, in the current study we used extrinsic incentives to manipulate subjects' motivation for detecting either new or old items. We use a modified version of the paradigm reported in Han et al. (2010). They were interested in why meta-analyses of the recognition fMRI literature consistently showed greater activation for hits compared to correct rejections in striatal regions traditionally associated with reinforcement learning and reward processing. In other words, much like the pupil old/new effect, there is a neural signal that robustly shows an old/new effect.

One possibility was that this activation reflected whether or not subjects were successful in recovering episodic content, causing greater activity for "old" relative to "new" reports. The logic underlying this idea is that retrieval of episodic content can act as a secondary reinforcer because it signals solution to a memory challenge. However, an alternate possibility considered was that observers typically viewed successful recognition as the goal of recognition testing more broadly. That is, because they are aware they are in a memory experiment they reasonably imbue positive recognition judgments with greater motivational significance relative to correct

rejections. Thus, striatal activation during recognition will depend on which response type is emphasized as important by a study's design. To test this, they crossed standard recognition with extrinsic reward manipulations designed to shift the goal from the detection of old items to the detection of new items. Participants completed a baseline block, a block during which "old" responses were incentivized and a block during which "new" responses were incentivized.

In the old-incentivized block old responses could win or lose \$1 depending on accuracy and "new" responses carried no monetary risk. Alternatively, in the new-incentivized block "new" conclusions carried monetary risk but "old" conclusions did not. This manipulation generated widespread moderation of the traditional activations associated with recognition. Specifically, in striatum the incentives governed with conclusion yielded more activation with the greater response for the incentivized recognition conclusion. This suggested that prior observations of striatal response were indeed a reflection of the different motivational significance subjects typically afford positive versus negative recognition conclusions in standard testing.

In contrast, in regions such as antero-lateral prefrontal cortex and lateral parietal cortex, that traditionally demonstrate greater activation for hits versus correct rejections, the incentive manipulation amplified (but never reversed) the traditional effect. In other words, incentivizing "new" conclusions eliminated the typical old > new effect in these areas while incentivizing "old" conclusions amplified (compared to baseline) the traditional effect.

### **1.3 Summary**

Overall, the Han et al. (2010) investigation reveals that modest incentive manipulations drastically altered the cortical and sub-cortical pattern typically observed during verbal

recognition. Returning to the current pupillometry focus, this raises the question of whether this manipulation of the motivation significance of recognition judgments would likewise alter the expression of the pupil old/new effect generating either an amplification pattern (as in PFC and lateral parietal) or a complete reversal pattern (as in striatum). More broadly, we tested whether we could modulate the pupil old/new effect using an incentive manipulation to alter the saliency of the probes. In the Discussion we explore how the attentional salience account of the pupil old/new effect accommodates the broader findings on recognition and pupil dilation and we also discuss the implications of replicating the finding of Mill, O'Connor and Dobbins (2016) that there are multiple functionally separable components that occur in each pupil dilation time course during a recognition trial.



## **Chapter 2: Method**

### **2.1 Participants**

Forty-one undergraduate students (13 male; mean age 20.2; range 18–26) enrolled in psychology courses at Washington University in St. Louis participated in this study in exchange for course credit. All subjects had normal or corrected-to-normal vision. This sample size was chosen prior to data collection because it is consistent with prior pupillometry studies involving recognition memory (Mill et al., 2016; Naber et al., 2013; Otero et al., 2011). Data from one participant was not included because of equipment malfunction, resulting in a final sample of 40 young adults (12 male; mean age 20.3).

### **2.2 Apparatus**

Pupil measurements were recorded using an EyeLink 1000 (SR Research, Mississauga, Canada) video-based eye tracker sampling at 1,000 Hz. Stimulus presentation was controlled by PsychoPy (Peirce, 2007) and PyGaze (Dalmaijer, Mathôt, & Van der Stigchel, 2014) on a 1,440 × 900 LCD monitor with a 75 Hz refresh rate. Participants' eyes were 65 cm away from the screen. Pupillary responses were recorded from the left eye, but vision was binocular.

### **2.3 Materials**

Stimuli consisted of 300 common nouns with an average of 6.76 letters, 2.37 syllables and 34.5 per million printed word frequency (Kucera & Francis, 1967). In order to minimize luminance differences between stimuli, all words were between four and nine letters in length. From this set of 300 words, three lists of 100 items (50 of which would be presented at encoding), were created for each participant by random assignment.

## 2.4 Procedure

In total, there were two study phases and three test phases (see Figure 1). The first study phase, made up of 50 items, was immediately followed by a 100-item recognition test phase. The second study phase was made up of 100 items and supported two subsequent 100-item test phases (see Figure 1). Importantly, there was no mention of the potential for reward until just before the second test phase; thus anticipation of performance-based reward did not influence pupillary responses recorded during the first test phase nor did it influence encoding for any of the stimuli.

Procedure	Incentive Manipulation	Method
STUDY Phase 1	No reward or feedback manipulation explained	50 words (syllable counting)
Recognition TEST 1		100 words (50 old/50 new)
STUDY Phase 2		100 words (syllable counting)
Instruction	Points, candy, & high score hall of fame explained	
Recognition TEST 2	“New” responses incentivized	100 words (50 old/50 new)
Recognition TEST 3	“Old” responses incentivized	100 words (50 old/50 new)

**NOTE:** Order of the incentive conditions in Tests 2 and 3 was counterbalanced across subjects.

*Figure 1.* Design schematic of the experimental paradigm.

Participants began by giving their informed consent and completing a brief demographic questionnaire. Participants then placed their head into a forehead and chin rest anchored 55 cm from the display monitor. They were informed of the importance of keeping their head still, told not to move from the headrest, and instructed to keep their eyes fixed to the center of the display as much as possible. The eye tracker was calibrated using a nine-point calibration procedure

immediately prior to each recognition test phase. The maximum error allowance for a single point was  $1.0^{\circ}$  and the average gaze error across the nine fixation points was  $0.5^{\circ}$  or less.

### **2.4.1 Encoding Phase**

During encoding, participants carried out a self-paced syllable counting task. Words were presented one at a time in the center of the screen. Participants were instructed to press the “Z” key for words with 1 or 2 syllables and to press the “M” key for words containing 3 or more syllables. Immediately following each response, a blank screen appeared for 250 ms. Participants were instructed to remember the words for an upcoming memory test.

### **2.4.2 Recognition Phase 1: Standard Old/New Recognition**

During each recognition test phase, 100 words (50 studied and 50 unstudied) were randomly mixed and presented serially in the center of the screen. Participants were instructed to decide whether each word was “old” or “new”. Each trial began with the presentation of a mask (XXXXX) in the center of the screen for 2000 ms. Then, this mask was replaced by a randomly drawn word from the test list and remained on screen for 4000 ms. Participants were instructed to press the “Z” key to indicate that they had seen the item during the study phase and to press the “M” key to indicate that they had not seen the item in the study phase. Participants were further instructed to indicate their confidence by pressing the response key 1, 2, or 3 times to indicate low, medium, or high confidence, respectively.

Following the recognition trial, a 1-point gaze contingent eye-tracker recalibration was performed (i.e., “drift correction”). If the gaze error was greater than 1 degree, a full nine-point recalibration was carried out before proceeding with the test. The first recognition test was immediately followed by the second encoding phase. Again, during the first recognition test and both encoding phases, there was no mention of any potential reward whatsoever. Thus, pupillary

activity during the first recognition test arguably reflects intrinsically rewarding task characteristics during recognition decisions. In addition, the potential for reward was only divulged after the second encoding phase, and therefore did not impact participants' strategies while encoding the to be remember words.

### 2.4.3 Recognition Phase 2: Old/New Recognition with Extrinsic Reward.

Following the second encoding phase, participants completed two successive recognition tests each of which was associated with a list of 100 items (50 studied and 50 unstudied). In each test reward was associated with a particular class of responses such that each participant completed one block wherein “new” responses were rewarded/punished and one block wherein “old” responses were rewarded/punished. In the remainder of the paper I will refer to these as the *new-incentivized* and the *old-incentivized* conditions, respectively. The order of the two incentivized blocks was counterbalanced across subjects.

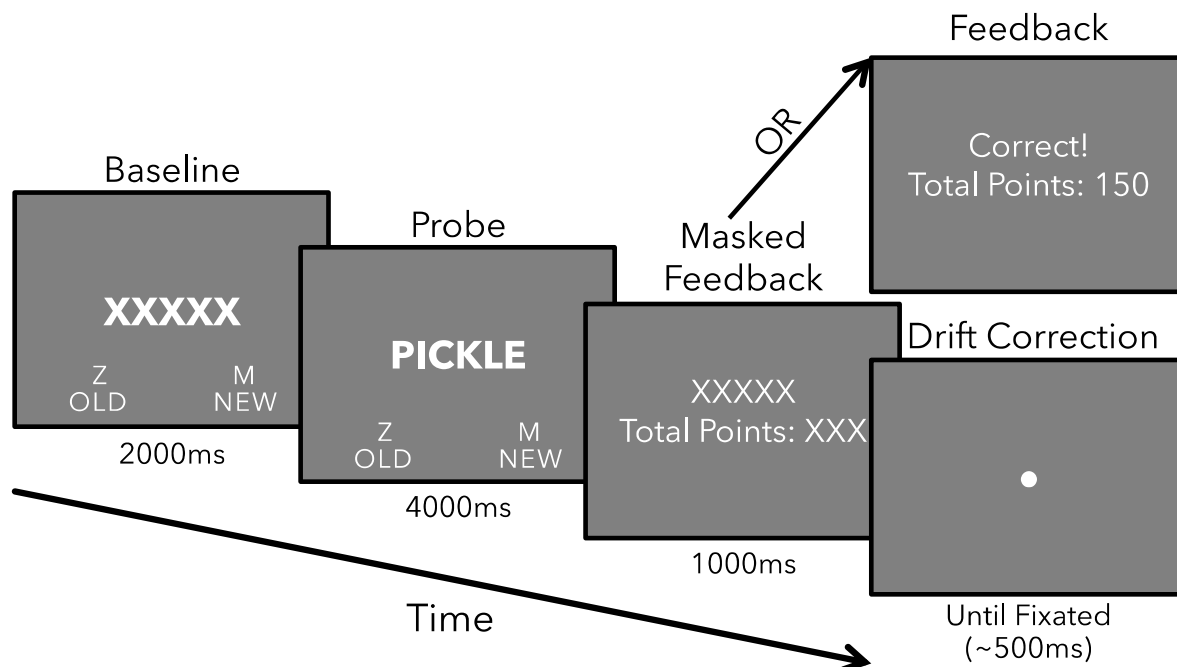


Figure 2. Example of one recognition test trial during an incentivized block.

**Points.** There were three components to the incentive manipulation: points, candy, and a high-score hall of fame. For the new-incentivized block, subjects were informed that they would gain 20 points for correct “new” responses (i.e., correct rejections) and lose 20 points for incorrect “new” responses (i.e., misses). In addition it was emphasized that they would not gain or lose points for “old” responses. For the old-incentivized condition, the same contingencies were applied to correct and incorrect “old” responses (i.e., hits and false alarms). Again, instructions emphasized that new responses would not gain or loss points. Importantly, this corresponds to a neutral payout in the context of signal detection decision models and therefore it is not expected to have an effect on response bias [i.e., the willingness to call something old; (Macmillan & Creelman, 2005)].

**Candy.** The instructions stated that at the end of the experiment, they could select one piece of candy for every 200 points they earned. A bowl of candy was in plain sight. Participants were informed that the highest possible score is 1000 points. At the end of the experiment, all participants were informed that the points did not actually have any contingency on how much candy they could have—everyone was encouraged to take as much candy as they wanted.

**Hall of Fame.** Lastly, participants were told that they could win a spot in the “hall of fame” of high scores. They were presented with a fictitious list of high scores and prompted to enter a user name that would be displayed with their score if it was high enough<sup>1</sup>. Note that neither their user name nor their actual scores were explicitly recorded; this ensured that all participants were presented with the same fictitious hall of fame and, more importantly, obviated

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<sup>1</sup> Anecdotally, our ambitious, young Wash U students seemed highly motivated by this possibility!

any concerns about anonymity and saving information about participants for display to other participants. There was a separate high score list for each incentivized block.

**Feedback.** For a subset of randomly selected trials, feedback was displayed centrally on the screen for 1000 ms indicating the accuracy of the response and a running total of points earned. Other trials did not include reward information after responding, but displayed a masked-feedback screen for 1000 ms such that trial timing was equivalent regardless of whether feedback was displayed or not (see Figure 2). Feedback was presented on 15% of the trials and could follow either response type. In this way, external feedback was not confounded with motivational saliency. Subjects were told that many of their responses would not receive subsequent feedback but that they would still gain or lose points consistent with the contingencies laid out for that block. Immediately following feedback (or the masked-feedback screen), a 1-point gaze contingent drift correction was performed prior to beginning the subsequent trial.

## **2.5 Preprocessing Eye-tracking Data**

Prior to analysis, pupillary data were preprocessed to remove blink artifacts (de Gee, Knapen, & Donner, 2014; Mathôt, 2013). All scripts for data analysis were written in R.

### **2.5.1 Blink Detection.**

For blink detection I closely followed Mathôt's (2013) approach. In Figure 3A, the uncorrected pupil signal for a single trial from a single subject is plotted as a continuous signal over 5000 ms (1000 ms of baseline followed by 4000 ms trial). The signal is measured in arbitrary units as outputted by Eyelink's software. In the figure, it is clear to see that the participant blinked twice during the trial. Eye blinks are characterized by a pronounced drop in

the pupillary signal, followed by a full loss of signal, and then usually a recovery artifact when the signal comes back online. In order to detect these events systematically, I calculated a velocity profile for each trace. However, the original signal is too noisy to create a reliable profile. In order to detect blinks efficiently, I began by smoothing the signal using a weighted moving window average of 10 samples (i.e., 10 ms). The resulting signal is plotted in Figure 3B.

Next I created a velocity profile by subtracting each sample from the immediately preceding sample in the signal (see Figure 3C). Blink onsets were subsequently identified as occurring when the velocity crossed a predetermined negative threshold (I selected -3 based on a visual examination of the data). This rapid decrease in pupil diameter corresponds to the apparent decrease in size of the pupil as the eyelid closes. Likewise, when the eyelid reopens there is a recovery artifact wherein pupil size rapidly gets larger. Thus, the algorithm detected the recovery period by indexing the time since onset that velocity exceed some positive threshold (I selected 1 based on visual inspection of the data). Finally, the offset was detected as the time at which velocity fell back down to 0. In this way, a blink corresponds to an onset, recovery, and offset index. According to Mathôt (2013), this detection algorithm underestimates the blink period by several milliseconds, thus I selected a margin value (15 ms) which was subtracted from the onset and added to the offset. In addition, “blinks” that were detected by the algorithm but lasted longer than 500 ms were not included as blinks (see below for handling missing data not caused by blinks).

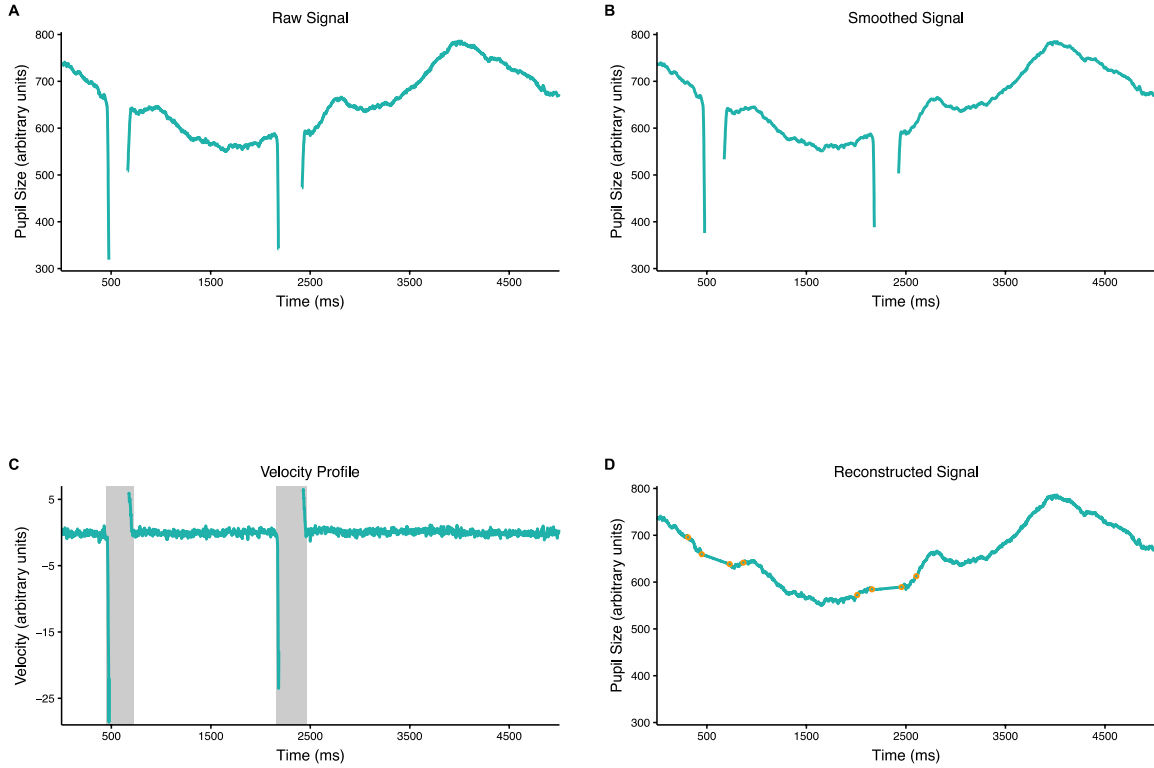


Figure 3. Blink reconstruction process.

## 2.5.2 Blink Reconstruction

For each blink, the duration of the blink was subtracted from the onset time and added to the offset time resulting in four equally spaced timepoints (see Figure 3D). Using these values, I extracted the associated signal from the original, unsmoothed trace, and fitted a linear interpolation of the signal. The resulting values that correspond to the two inner timepoints (blink onset and offset) are then used to replace the values in the original data.

Taken together, the algorithm required four subjective parameters: the amount of smoothing (10 ms weighted moving average), the negative velocity threshold (-3 arbitrary units)



for detecting onset, the positive velocity threshold (1 arbitrary unit) for detecting recovery, and the temporal margin around the blink to interpolate as well ( $\pm 15$  samples).

### **2.5.3 Other Missing Samples**

In addition to blinks, other signal dropout occurred. Trials missing 20% or more of the samples (after blink correction) were excluded. This resulted in a loss of 1% of the total trials across all subjects. Any remaining missing samples (i.e., for trials with less than 20% of missing data), were simply replaced by the mean pupil size for that trial. Finally, to reduce data for statistical analysis, pupil dilation was down-sampled from 1000 Hz to 100 Hz.

### **2.5.4 Baseline Correction**

For each trial, I calculated the mean pupil dilation during a 1000 ms baseline period (immediately preceding the presentation of the memory probe) and subtracted this value from each sample of the time course (de Gee et al., 2014; Laeng, Ørbo, Holmlund, & Miozzo, 2011). Then, in order to normalize the scores, I divided the time course by the baseline grand mean. That is, for each subject I calculated a mean for the 1000 ms baseline period across all trials. This normalization procedure transformed the pupil signal into units of percent modulation, which is useful because we are primarily interested in the differential effects of the within-subject manipulation (i.e., incentive) on pupillary response.

## **Chapter 3: Results**

### **3.1 Behavior**

#### **3.1.1 Hit Rates**

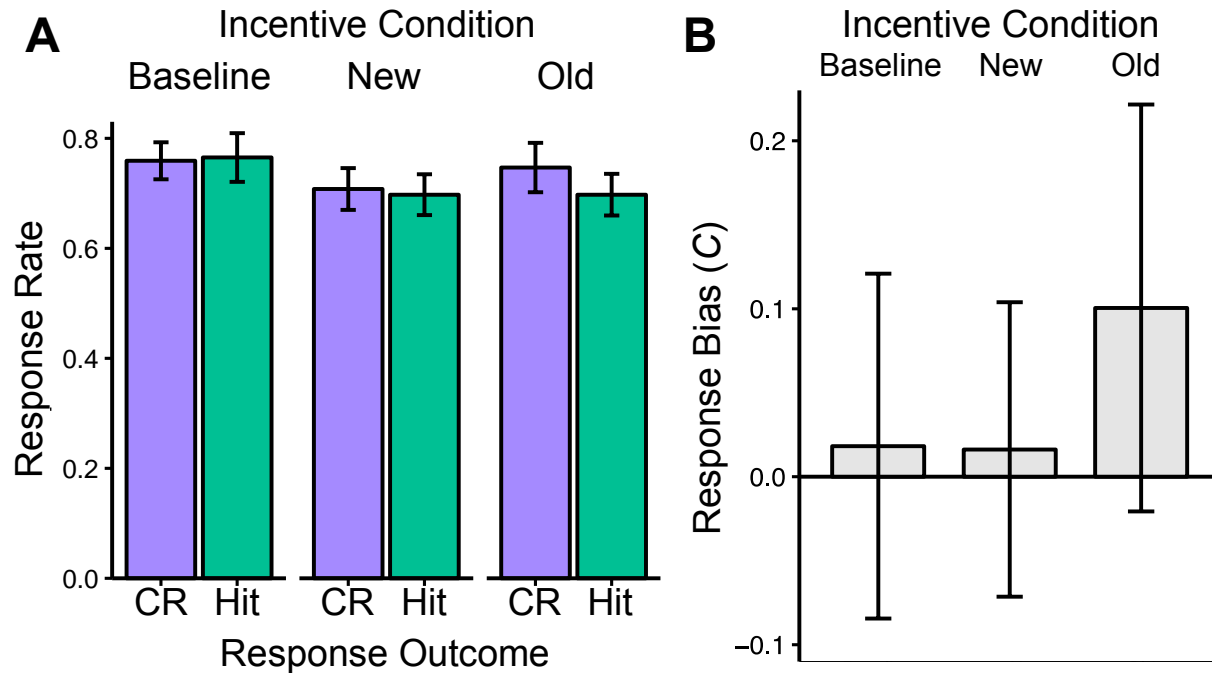
Hit rates (the proportion of old words identified as “old”) and correct rejection (CR) rates (the proportion of new words identified as “new”) are presented in Figure 4. A within-subjects, one-way ANOVA with Incentive Condition (control, new-incentivized, or old-incentivized) entered as a factor revealed a significant effect of incentive on hit rate ( $F_{(2,76)}=4.85$ ,  $MS_e=.06$ ,  $p=.010$ ). As you can see in Figure 4, this finding seems to be driven by a difference in hit rates between the control condition and the two incentivized conditions. It is worth noting that the control condition was always first, whereas the order of the subsequent incentivized blocks was counterbalanced. It is possible that performance in the control block benefitted from this whereas any fatigue and interference effects are presumably equated in the two incentivized blocks. Consistent with this idea, Tukey’s HSD test showed that hit rates in the control block were significantly higher than hit rates in the two incentivized blocks ( $p=.0193$  and  $p=.0191$ , respectively) and, importantly, there was no difference in hit rates between the two incentivized blocks ( $p=.999$ ).

#### **3.1.2 Correct Rejection Rates**

Correct rejection (CR) rates were similarly analyzed and revealed a significant effect of incentive on correct rejection rate ( $F_{(2,76)}=3.32$ ,  $MS_e=.03$ ,  $p=.042$ ). Tukey’s HSD test showed that the difference in correct rejection rates between the control condition and the new-incentivized condition was marginally significant ( $p=.037$ ). There was no difference in correct rejection rates between the control condition and the old-incentivized condition ( $p=.827$ ) nor between the two incentivized conditions ( $p=.145$ ).

### 3.1.3 Bias

Next, response bias ( $C$ ) was analyzed using a within-subjects, one-way ANOVA with Incentive Condition entered as a factor. There was no significant effect of incentive condition on bias ( $F_{(2,74)}=1.27$ ,  $MS_e=.09$ ,  $p=.287$ )<sup>2</sup>.



*Figure 4.* Memory outcomes and bias. Panel A shows the mean response rates ( $\pm 2$ \*standard error of the mean) of correct rejections (CR; purple bars) and hits (green bars) as a function incentive condition. Panel B shows the mean bias values ( $\pm 2$ \*standard error of the mean) as a function incentive condition.

### 3.1.4 Confidence

A Response Type (Hits, CRs) by Incentive Condition (Control, New-Incentivized, Old-Incentivized) repeated-measures ANOVA on average confidence ratings revealed main effects of

<sup>2</sup> One further subject who made no false alarms in one incentive condition was removed from the  $C$  analysis as this measure could not be calculated for the condition.

Incentive Condition ( $F_{(2,73)}=19.84$ ,  $MS_e=63.07$ ,  $p<.001$ ) and Response Type ( $F_{(1,36)}=30.56$ ,  $MS_e=85.40$ ,  $p<0.001$ ). The Incentive by Response interaction was not significant ( $F_{(2,76)}=.85$ ,  $MS_e=1.02$ ,  $p=.43$ ). The main effect of response type is driven by the tendency for hits to garner higher confidence ratings than do CR. The main effect of Incentive Condition is driven by overall more confident ratings in the control condition compared to each of the two incentivized conditions. Importantly, however, there was no effect of Incentive Condition on average confidence when the analysis was re-run with only the incentivized conditions ( $F<1$ ).

### 3.1.5 Reaction Time

The same two-way repeated measures ANOVA on reaction time (RT) also revealed main effects of Incentive Condition ( $F_{(2,75)}=29.46$ ,  $MS_e=29.28$ ,  $p<.001$ ) and Response Type ( $F_{(1,37)}=14.39$ ,  $MS_e=11.81$ ,  $p<0.001$ ). The Incentive by Response interaction was not significant ( $F_{(2,78)}=1.51$ ,  $MS_e=.78$ ,  $p=.23$ ). The main effect of Response Type is driven by the tendency for RTs to be faster for hits than for CRs.

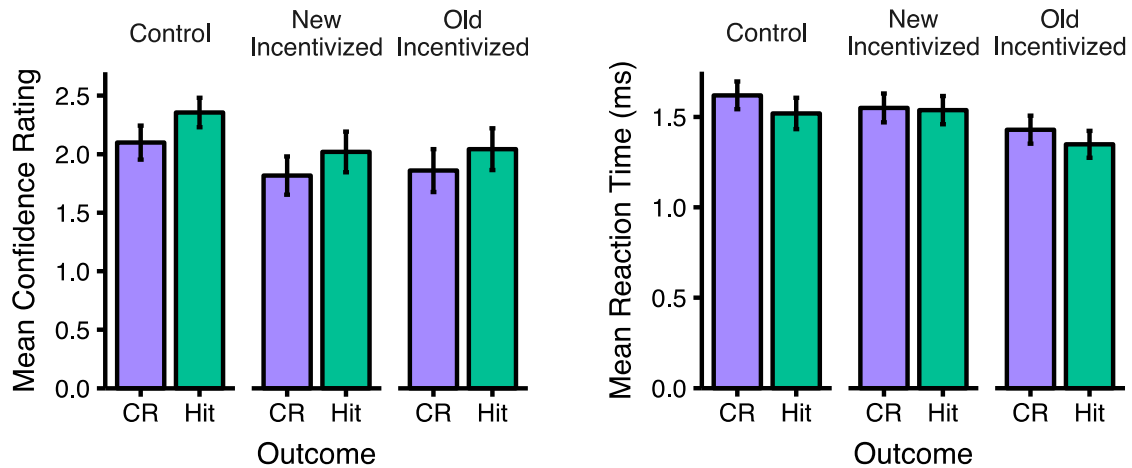


Figure 5. Mean confidence ratings (panel A) and reaction times (panel B) of correct rejections (CR; purple bars) and hits (green bars) as a function incentive condition (+/- 2\*standard error of the mean).

## 3.2 Pupillary Response Analyses

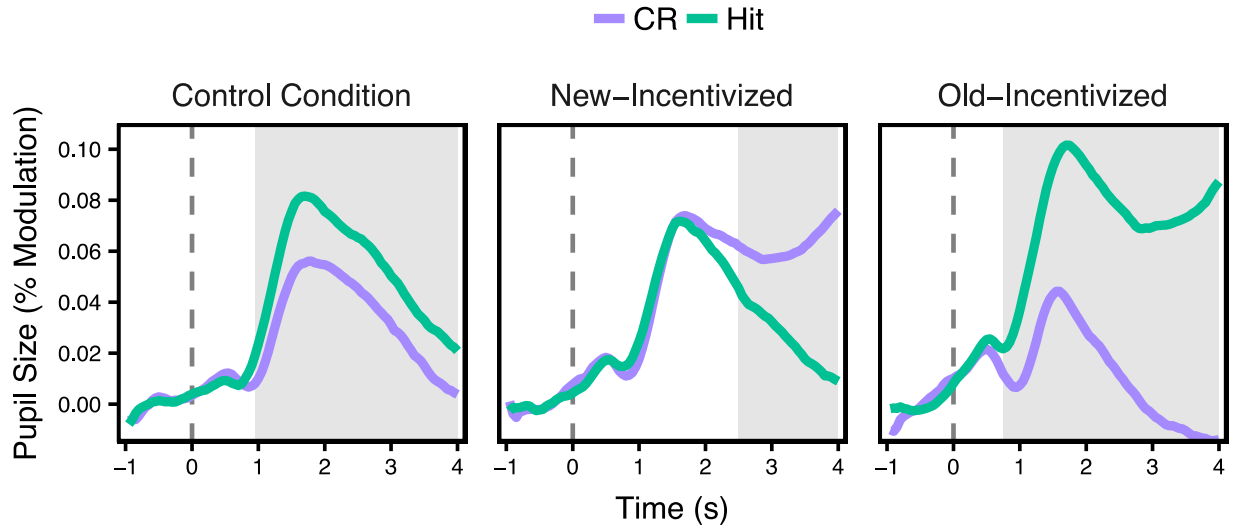
In each of the pupil timecourse plots presented below, the three panels correspond to the three incentive conditions (baseline, new-incentivized and old-incentivized), the dotted vertical line denotes the onset of the test probe and the shaded regions denote where the signals differed significantly according to paired samples t-tests for each timepoint with p-values adjusted for family-wise error using the false discovery rate procedure at .05.

### 3.2.1 The Effect of Incentives on the Old/New Pupil Response

Figure 6 illustrates the trial-locked mean pupil response timecourse for hits and correct rejections in each incentive condition. Beginning with the baseline condition, the pupil old/new effect is clearly replicated. Approximately 1000 ms following the appearance of the recognition probe, the dilation timecourse begins to differentiate between old and new responses such that items judged “old” garner greater pupillary dilation than do items judged “new”. This difference peaks at about 1800 ms after which both time courses return to baseline at a similar rate.

In the new-incentivized condition (middle panel, Figure 6), the early pupil old/new effect has been completely eliminated. When subjects are motivated to maximize the detection of new material, the period from stimulus onset to peak response shows no measurable difference between hits and correct rejections.

Turning to the old-incentivized condition, the early pupil old/new effect is clearly amplified compared to baseline, and indeed differences are detectable as early as 800 ms post stimulus onset. As a result of this amplified effect, the difference between the signal peaks is noticeable larger than in the baseline condition.



*Figure 6.* Trial locked pupillary timecourses for accurate memory responses. Shaded regions represent significant differences between hits (green lines) and correct rejections (CR; purple lines), using paired t-test and false-discovery rate correction.

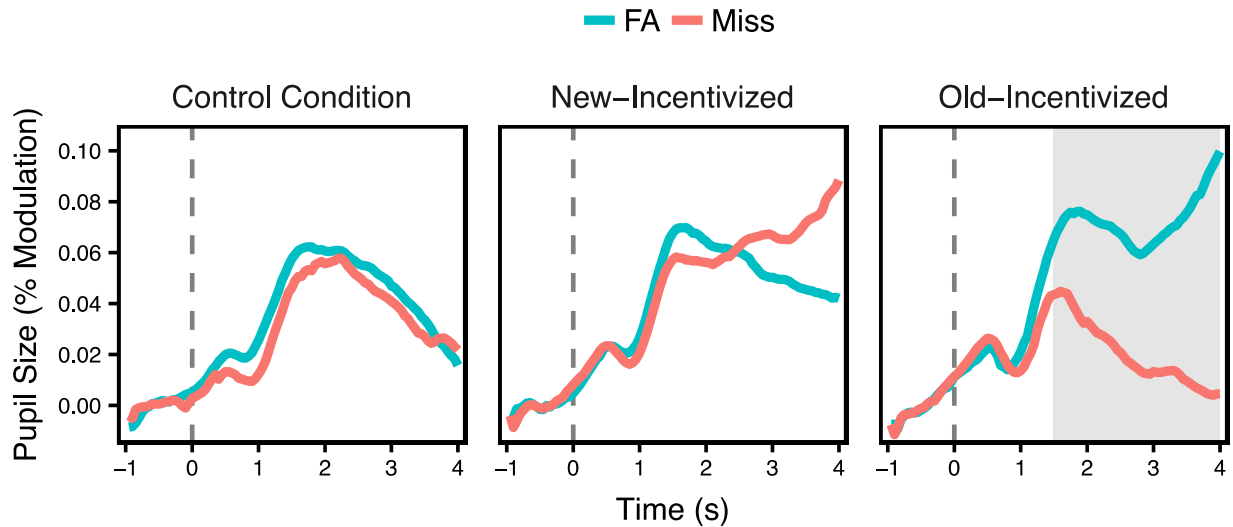
### 3.2.2 A Dissociable Goal-Contingent Response

Aside from the modulation of the pupil old/new effect in the portion of the dilation time course spanning stimulus onset to its peak at about 1800 ms, Figure 6 also shows a novel component not present in Mill, O'Connor and Dobbins (2016) or, as far as we can tell, elsewhere in the literature. This component, which we are terming the incentive consistent response (ICR) reflects a late secondary dilation that occurs only for responses that are consistent with the external incentives in the incentivized block. Looking at Figure 6 this response is reflected in the upturn in the dilation time course beginning at about 2500 ms for new responses under the new-incentivized block and old responses under the old-incentivized block. The size of the upturn is similar for the old-incentivized and new-incentivized blocks and yet the early old/new effect is prominent for the former yet absent in the latter. Moreover, we know that this is a post response

effect because the average RT in these two conditions is 1603 ms and 1427 ms respectively, which is well before the upturn. In contrast, the pupil old/new effect is detectable as early as 800 ms in the old-incentivized condition, which is well before the average response time. Thus, the two effects constitute two psychologically distinct phenomena occurring in the pupil dilation time course.

### 3.2.3 Incorrect Memory Responses

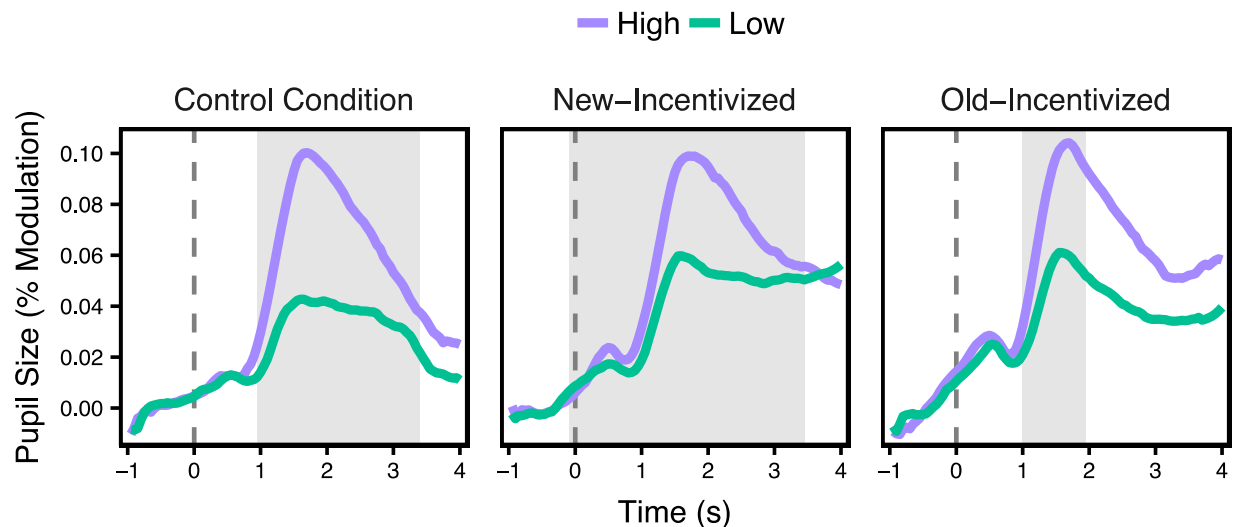
Turning to Figure 7 we examine the dilation time courses in an analogous manner but focusing instead on incorrect reports. Although the old/new effect is generally absent during the Control Condition, it is clear that the modulation of the old/new effect and the incentive consistent response (ICR) effect are both replicated for incorrect responding. Thus the phenomenon reflect the subjective recognition experience of the observers and their conclusions regardless of their accuracy.



*Figure 7.* Pupil traces for incorrect responses. Shaded regions represent significant differences between false alarms (FA; blue lines) and misses (red lines), using paired t-test and false-discovery rate correction.

### 3.2.4 Subjective Uncertainty and Reaction Time Effects

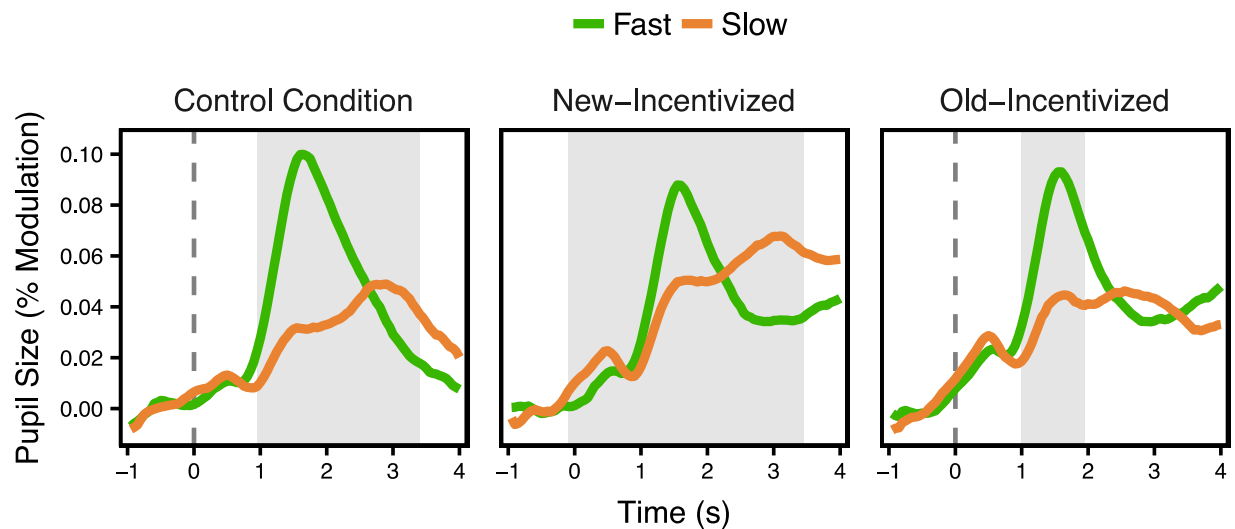
Mill, O'Connor and Dobbins (2016) isolated a pupillary component they concluded reflected decision uncertainty. More specifically, rapid conclusions (regardless of whether they were 'old' or 'new') were associated with an early peak and a strong negative slope. In contrast, slow conclusions were associated with a diminished early peak and a sustained dilation response. In that study, this pattern was unaltered by the cueing conditions in place and thus reflected a general characteristic of judgment ease or uncertainty independent of subjective expectations. Although they labeled the effects as subjective uncertainty, that study did not collect subjective reports of confidence. Instead, because this pattern occurred for reaction time and an analogous pattern was seen when comparing erroneous versus correct responding, it was concluded it reflected subjective decision uncertainty. In the current report we collected subjective confidence, and so can contrast low with high confidence across the three incentive conditions.



*Figure 8.* Pupil traces as a function of confidence. Shaded regions represent significant differences between high confidence (purple lines) and low confidence (green lines), using paired t-test and false-discovery rate correction.



Figure 8 demonstrates that indeed high confidence responses are more peaked with a strongly negative slope whereas low confidence responses are less peaked with a sustained or flatter slope. Critically, this pattern is consistent across the three incentive conditions and thus reflects a general characteristic of the judgments. In other words, comparing Figure 6 to Figure 8 it is clear that the early pupil old/new effect is incentive contingent, however the current high/low confidence effect is not. To further isolate whether this effect corresponds to the subjective uncertainty response discussed by Mill and colleagues, we followed their procedure of breaking reaction times of trials (regardless of accuracy and type of response) into quartiles. Figure 9 below plots the fastest and slowest quartiles across the three incentive conditions.



*Figure 9.* Pupil traces as a function of high and low reaction time. Shaded regions represent significant differences between fast reaction times (green lines) and slow reaction times (orange lines), using paired t-test and false-discovery rate correction.

Under this format we see that the quickest responses are peaked with prominent negative slopes and the slowest responses are not peaked but display sustained or slightly positive slopes.

As with confidence these patterns are fairly consistent across the three incentive conditions and hence this effect is clearly distinct from the old/new effect isolated earlier.

### **3.3 Results Summary**

In summary, the trial locked pupillometry replicates and extends the findings of Mill, O'Connor and Dobbins 2016. First, we demonstrate, consistent with an attentional salience interpretation, that the old/new effect is completely moderated by the motivational significance of positive recognition evidence. It is eliminated when new responses are incentivized but amplified when old responses are incentivized. Critically, the accuracy and bias of subjects in these two incentive conditions is quite similar and so the effect is not a secondary consequence of somehow altering the availability of memory information or the manner in which it is used. As we expand upon in the discussion, this confirms the broader notion that early in the time course of pupil dilation, the response reflects the degree to which recovered memory signals are attentionally salient.

The second finding linked to Mill, O'Connor and Dobbins (2016) is the confirmation that subjective confidence modulates the dilation time course irrespective of salience manipulation. Above it is clear that the peak and slopes of the low versus high confidence responses differ considerably regardless the incentive conditions; a pattern similar to what is seen when the responses are instead binned by speed in order to compare slow and fast responding. This converges on the assumption that the response captures subjective uncertainty.

Finally, the data demonstrate a new component, the incentive consistent response (ICR) that occurs post-response and is restricted to responses that carry future outcome consequences.

As we discuss below, these may reflect mechanisms critical to operant learning and response evaluation.

## **Chapter 4: Discussion**

The current data demonstrate an important dissociation in the PD response during episodic recognition and challenge the functional interpretation of the pupil old/new effect as a marker of retrieval or memory strength. As discussed in the Introduction, the prevailing view is that the pupil old/new effect is an index of memory strength reflecting the effort required to recover content from memory (Goldinger & Papesh, 2012; Võ et al., 2008). However, recent work by Mill, O’Conner and Dobbins (2016) demonstrates that the old/new effect can be completely modulated by participants’ expectations, suggesting that the old/new effect reflects attentional saliency and not episodic recovery. In this study we provide further support of this idea by manipulating attentional saliency of recognition evidence with performance-based incentives.

### **4.1 Toward a New Model of the Pupil Old/New Effect**

Memory retrieval is typically a goal-directed behavior and in this study we tested the idea that the pupil old/new effect in recognition memory is modulated by subjects’ interpretation of the goals of the memory task. Specifically, subjects might intrinsically value “old” conclusions relative to “new” conclusions based on a reasonable assumption that detecting studied items is the primary goal in a recognition task. In the current study, we demonstrated that the pupil response during a typical verbal recognition showed greater activation for correct responses to old items (i.e., hits) compared to correct responses for new items (i.e., correct rejections). Critically however, this pattern was altered by the addition of extrinsic incentives, eliminating the effect when incentives were linked to new responses and amplifying the effect when incentives were linked to old responses. This finding seriously undermines any account that

suggests PD indexes a pure signal of memory strength and furthermore raises the possibility that the pupil old/new effect in other recognition studies was in fact driven by subjects' intrinsic goals to maximize the detection of studied material relative to novel material.

This line of logic does raise an important question: why is the pupil old/new effect amplified when rewarding old responses relative to the baseline condition? Indeed, I argue that in both cases subjects are motivated to detect old material as compared to novel material. However, the goal is most certainly more ambiguous in the baseline condition. While some subjects might prioritize the detection of old materials, others may not. It is only when the subjects are in the old-incentivized condition that the goal of maximizing the detection of studied items is explicit. Importantly, we are arguing that PD reflects a contextually specific response driven by attentional saliency, and that at baseline, subjects *might* value “old” conclusions based on an assumption that the primary goal in a recognition memory task is to maximize the detection of studied items. In contrast, if PD was specific to recollection, memory strength or recovery of episodic detail, then one would have predicted that regardless of the external contingencies, hits always led to more activation than correct rejections—a prediction that both the current data and Mill, O’Conner and Dobbins (2016) found to be invalid.

Our findings showed that the old/new effect could be modulated by the observers’ context specific goals/motivation. Furthermore, we identified 3 dissociable components that are present in the PD responses: the early “old/new” signal, the subjective confidence component, and the late incentive-consistent response signal (ICR). Next, I consider each of these in turn.

#### **4.1.1 The Early Attentional Component**

Mill, O’Conner and Dobbins (2016) used cued expectations to demonstrate that the pupil old/new effect reflected an orienting phenomenon tied to the attentional salience of recognition

memory signals. This conclusion follows from research in visuospatial orienting where manipulations of cue validity produce both behavioral and neurophysiological effects. In general, as average endogenous cue validity increases, reaction times to valid trials decreases whereas reaction times to invalid trials increases (Jonides, 1980; Posner, 1980; Posner & Petersen, 1990).

One way to view this effect is as a manipulation of the degree of surprise or salience of information when invalidly cued, and consistent with this Vossel, Thiel, and Fink (2006) showed that activation to invalidly cued objects in a Posner detection task was heightened in lateral parietal and posterior-lateral PFC regions for 90% compared to 60% valid cue conditions. In other words, the response to the presentation of the target at an invalidly cued location was heightened as a function of how unexpected its appearance there was. This pattern is also potentially consistent with the model of Corbetta and Shulman (2002) in which lateral temporo-parietal and ventrolateral prefrontal regions are thought to contribute to the detection of unexpected, behaviorally relevant or salient stimuli and are critical for the resetting or breaking of expectations.

However, the above models were developed in the domain of visuospatial processing not memory processing. Extending this framework to recognition memory, the prediction is that activations in response to recognition evidence should be sensitive at the level of individual trials. Using fMRI and the explicit cueing paradigm discussed previously, our research group has demonstrated that they are (Jaeger, Konkel, & Dobbins, 2013; O'Connor et al., 2010). For example, left angular gyrus demonstrated a marked amplification of the typical retrieval success effect (hits > correct rejections) when participants were cued that recognition was unlikely, but this effect was fully eliminated when they were cued that recognition was likely (Jaeger et al., 2013). Moreover, list-wise manipulations of old item probability also moderate the parietal

response to old versus new items such that as the probability of encountering old items decreases, the activation in response to these increasing rarer stimuli increases (in comparison to new materials) in lateral parietal cortex (Herron, Henson, & Rugg, 2004).

The current findings converge with the above behavioral and neurophysiological findings in suggesting that the early PD old/new response tracks the attentional salience of recognition signals. However, instead of modulating salience through cue manipulations, we manipulated the motivational significance of recognition evidence using a paradigm previously demonstrated to influence recognition fMRI activations in prefrontal, parietal and striatal regions (Han et al., 2010). In other words, we successfully “turned-up” and “turned-down” the attentional salience of memory signals using extrinsic incentives rather than unexpected outcomes. Moreover, because participants only received feedback on 15% of the trials, and feedback followed either response type, manipulating attentional saliency to particular memory signals did not depend on the immediate receipt of reward or feedback.

#### **4.1.2 Confidence/Certainty Component**

Analysis of high versus low confidence traces revealed a distinct pupillary component that tracked a general signal of uncertainty. This signal was not at all dependent on the motivation manipulation or response selection, thus suggesting it indexes judgment uncertainty in a general fashion, and in this sense is consistent with the findings reported in Mill et al., (2016). Critically, without decomposing the trial-wise dilation response into two components this link with decision effort/uncertainty would have been less clear.

#### **4.1.3 Incentive-Consistent Response (ICR)**

The late pupillary response observed for incentive consistent responses is—as far as we know—a novel finding in the memory literature. We speculate that this may reflect a

reinforcement learning type mechanism consistent with the imaging data in Han et al., (2010). For example, Tanaka, Balleine and O'Doherty (2008) used fMRI to assess the neural mechanisms involved in subjects' ability to accurately assess and adapt to the causal effectiveness of their behaviors in a changing environment. They scanned subjects while they pressed a button to earn money. The response–reward relationship continued to change over time. Subjects' judgments about the causal efficacy of their actions reflected the objective contingency between the rate of button pressing and the amount of money they earned. They found that medial prefrontal cortex tracked local changes in action–outcome correlations, implicating this region in the on-line computation of contingency.

Similarly, de Gee, Knapen, & Donner, (2013) reported that pupil dilation during decision formation was bigger before yes than no choices, irrespective of the physical presence of the target signal. Remarkably, the magnitude of this pupil choice effect reflected the individual criterion: it was strongest in conservative subjects choosing yes against their bias. Thus PD reflects how the behavior (i.e., decision) relates to the decision maker's attitude/context.

Lauwereyns et al. (2002) made a case that caudate activity signals learned responses biases. These researchers capitalized on the fact that caudate neurons tend to demonstrate preferred directions in the contralateral hemisphere. During blocks in which this direction was associated with reward on half of the trials, these neurons demonstrated increased responses prior to the appearance of targets whereas this pre-target activity was muted when the ipsilateral direction was instead linked to reward. Based on these findings Lauwereyns et al. (2002) suggested that the caudate biases responding in advance of the target presentation as a function of prior reward histories, which in effect would yield a different baseline for executing the reward-linked versus non-reward linked responses.



Although it's only speculation, given the studies reviewed here, this late response to executing incentivized responses may have to do with subjects' ability to accurately assess and adapt to the causal effectiveness of their behaviors in a changing environment.

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